

The Effects of Flow on Polyp-Level Prey Capture in an Octocoral, *Alcyonium siderium*

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Abstract. Particle capture by individual polyps and tentacles of the octocoral, *Alcyonium siderium*, was investigated in flows of different speed and turbulence intensity. In low flow ($U_{\text{mean}} = 2.7$ cm/s; $u' = 1.2$ cm/s, where u' is the root mean square of the fluctuations from U_{mean}), tentacles on the upstream side of a polyp capture the most prey. In intermediate flow ($U_{\text{mean}} = 12.2$ cm/s; $u' = 6.0$ cm/s), downstream tentacles within a polyp catch the most prey. In high flow ($U_{\text{mean}} = 19.8$ cm/s; $u' = 4.0$ cm/s), polyps are bent downstream, eddies form over the tentacular surfaces, and the capture distribution over tentacles becomes radially symmetric. At all flow speeds tested, particles are caught with increasing frequency nearer the tip of the tentacle relative to locations near the pharynx. At the highest flow speed tested, no particles are caught on the segment of each tentacle closest to the pharynx. The per polyp capture efficiency is low and drops markedly with increasing Reynolds number. The capture mechanism for this species appears to be direct interception; inertial impaction is shown to be unimportant. Flow modulation of particle capture by polyps is probably a general phenomenon among octocorals.

Introduction

The application of modern engineering theory to the analysis of particle capture by suspension feeding organisms began with a review of the engineering and fluid mechanics literature by Rubenstein and Koehl (1977). The medical community has long been interested in the related problem of how particles are deposited in the tracheobronchial tree of mammalian lungs (Findeisen, 1935; Landahl, 1950, 1963). The theory invoked was the same (McMahon *et al.*, 1977), and importance of flow pattern in affecting the location of particle capture inside lungs

was recognized (Bell, 1974). Particle capture mechanisms used by biological filters include direct interception (the particle comes within one particle radius of a filtering surface), inertial impaction (the particle contacts the filter because particle inertia causes it to deviate from a fluid streamline around the filter), diffusive deposition (both Brownian and eddy-enhanced—the motion of the particle across streamlines leads to contact with the filter), sieving (the particle is too large to pass through gaps in the filter geometry), electrostatic attraction (requires net surface charges of opposite sign on filter and particle), and gravitational deposition (a particle denser than the fluid sinks and contacts the filter). Aerosol filtration theory allows estimation of the relative importance of these mechanisms by calculating the ratios of relevant forces acting on particles of different charge, size, and density, in flows of different velocity and viscosity (LaBarbera, 1984).

Recent work in organisms as diverse as conifers (Niklas, 1982a,b), dipteran larvae (Ross and Craig, 1980), polychaetes (Taghon *et al.*, 1980; Merz, 1984), veliger larvae of mollusks (Strathmann and Liese, 1979), ophiuroids (LaBarbera, 1978), bryozoans (Okamura, 1984, 1987), hydroids (Harvell and LaBarbera, 1985; Hunter, 1989), and crinoids (Holland *et al.*, 1987) has extended our knowledge of how biological filters work and how flow speed can affect the geometric pattern of particle capture at the level of the colony or individual. An important generalization from these works is that the coupling between an organism's filter morphology and the resulting flow field, whether generated actively or passively, is extremely important in the particle capture process.

Few studies have examined the mechanics of zooplankton capture by passive suspension feeding cnidarians at the level of the filtering elements themselves, the polyps composed of tentacles. Lewis and Price (1976) investigated mucus feeding in corals. Hunter (1989) demonstrated that feeding effectiveness of hydroid polyps was greater in os-

cillatory flow compared to steady, unidirectional flow. Harvell and LaBarbera (1985) examined how flexibility affects local flow speeds over polyps in hydroid colonies. Best (1988) has investigated prey capture in the sea pen, *Ptilosarcus gurneyi*, a species that has the polyps arranged at the ends of cantilevered support tissue through which flowing seawater passes. She found that the deformability of the organism strongly affected filtration efficiency and volume of water filtered; in effect the organism could tune its feeding performance by maintaining a variable porosity filter.

While some workers have investigated the location of prey capture on the surface of cnidarian colonies (Lev-ersee, 1976; Lasker, 1981; Patterson, 1984), no studies have addressed the location of prey capture within individual polyps or tentacles. *Alcyonium siderium* Verrill is a planktivorous colonial octocoral common on hard rock substrate in the New England subtidal (Sebens, 1986). Its diet consists largely of small zooplankton; invertebrate eggs, foraminiferans, ascidian larvae, nematodes, harpacticoid and calanoid copepods, barnacle nauplii and cyprids, ostracods, and crustacean fragments were common, although algal material is often present (Sebens and Koehl, 1984). It readily captures and eats live zooplankton and *Artemia* cysts in a laboratory flume (Patterson, 1984). Prey capture events by individual tentacles are easily observed by the naked eye. The subtidal habitats it occupies can differ greatly in water motion (Sebens, 1984; Patterson, 1985), and there is a change in colony morphology of local populations that is correlated with flow regime, with finger-like colonies found in slower flow areas, and lobate ellipsoids and roughly spherical forms found in higher flows (Patterson, 1980). The present study tested whether the location of prey capture within individual polyps and tentacles of the boreal octocoral, *Alcyonium siderium*, is affected by flow patterns over the colony.

Materials and Methods

Colony collection, maintenance, and flow generation and measurement

Polyp feeding experiments were conducted at the Marine Science Center (MSC), Northeastern University, Nahant, Massachusetts, and at the University of California, Davis. Colonies of *A. siderium* were collected and maintained in flowing seawater tables or recirculating chilled aquaria. A recirculating Plexiglas flume (98 liters; 15 cm × 15 cm working section; 1.9 m long) patterned after a design published by Vogel and LaBarbera (1978) and equipped with a chiller (Aquaneitics) enabled colonies to feed in flows of various speeds and turbulence intensities at 15°C. Patterson (1984) gives a quantitative description of flow in this particular flume. All experiments were performed with the flow straighteners removed, resulting in

higher turbulence in the flow tank and a closer approximation to the flow seen over the colonies in the field (Patterson and Sebens, 1989). Seawater for the flume was obtained from the MSC seawater system and was filtered twice (sand, cotton mesh) to remove particles greater than 20 µm diameter or was made fresh using InstantOcean, and adjusted to a salinity of 34‰.

Flow speeds and turbulence intensities were measured with a two channel thermistor flowmeter circuit modified from LaBarbera and Vogel (1976). The frequency response of the probe plus circuit is 5 Hz at -6 dB down from maximum response. The turbulence intensities may underestimate the true turbulence in the flume, if there is significant energy at frequencies above 5 Hz; this aspect of flume flow regime was not evaluated. The velocity signal was converted into an FM signal for transmission over a distance of several meters to a frequency-to-voltage (f/v) convertor. The output of the f/v convertor was sent to a signal conditioner (custom-made) and eight bit successive approximation A/D convertor (Mountain Computer) connected to an Apple IIe microcomputer. The sampling rate was 10 Hz.

Octocoral colonies attached to mussels (*Modiolus modiolus*) were collected subtidally. Mussel shell fragments bearing *Alcyonium* were mounted securely in the flow tank working section. The prey offered to the colonies were cysts of the brine shrimp, *Artemia*. Characteristics of the cysts are described in Patterson (1984). The cysts are about the same size as the mean prey size taken by *Alcyonium* in the field (Sebens and Koehl, 1984).

Location of prey capture

The spatial location of prey capture on individual polyps of *Alcyonium* was studied in flows of high turbulence levels and differing mean flow speeds. Colonies used ranged from 2 to 8 cm in greatest dimension when expanded. Colonies were all roughly spherical. Prior to an observation period, a single colony was introduced to the flow tank and allowed to acclimate to the flow regime and expand its polyps. A standard volume of seawater (1l) and weight of hydrated cysts (0.45 g) were added to the flow tank at the beginning of the observation period. The flow 1 cm above the observed polyp was adjusted to have a mean value of 2.7, 12.2, or 19.8 cm/s (4 s average achieved through an electronic integrator) by adjusting the speed control on the flume motor. Five minutes into the experiment, three 60-ml samples were withdrawn isokinetically (Brodkey and Hershey, 1988) using a Cole-Parmer peristaltic pump (model no. 7568) smoothed with hydraulic capacitors. Each sample was filtered onto grid- ded Millipore filters, the cysts counted, and the mean concentration of particles calculated. The range of particle concentrations encountered by the colony among experiments ranged from 0.13 to 0.53 cysts/ml.

Figure 1A shows a typical top view of a polyp after a feeding bout and the coordinate system used to assess location of capture around the polyp's circumference. Note that the coordinate system for the top projections paired tentacles from the bilaterally symmetric halves of the polyp (Fig. 1A). The coordinate variable (x) used for describing capture along individual tentacles is shown in Figure 1B; note that the distance along the tentacle (x) is normalized to the tentacle length (L). Capture events on individual polyps were observed at a magnification of $35\times$ through a dissecting microscope suspended over the flume. A watch glass floating on the water and anchored over the colony prevented blurring of the image from capillary waves at the air/water interface. As a feeding bout progressed, composite maps of capture sites of cysts from individual polyps were made (Fig. 1A). All polyps censused were located near the top of the colony; polyps chosen for observation had their tentacles oriented to the flow (Fig. 1A).

An ocular micrometer permitted measurement of relative position of capture along the length of a tentacle. Only particles caught on the oral side of the tentacles were noted; particles were very rarely captured on the aboral side of the tentacles. The tentacle capture maps were divided into five non-dimensional length sectors. Particle counts in the tentacle length sectors were normalized within a tentacle to the projected area available for particle capture. Surface areas of polyps were computed using a camera lucida and an interactive digitizing tablet (Apple Graphics Tablet). The area of the pinnules was not measured in calculating areas available for capture. Projected surface area of the entire colony was measured similarly.

Feeding efficiency

A dimensionless measure of feeding effectiveness, the efficiency of prey capture at the polyp level was computed as follows: the number of particles caught per polyp during a standard feeding bout was divided by the number of particles passing through the cross-sectional area occupied by the colony (divided by the number of polyps), if the colony were not there. This result is the standard definition of filtration efficiency from engineering theory (Dorman, 1966). The number passing through the cross-sectional area was calculated by integrating the flow over the height and width of the colony and multiplying by the sampled particle concentration. Feeding rate in the dense concentrations of prey used in the flume is not constant, but decreases with time (Patterson, 1991). These concentrations were similar to zooplankton patch concentrations in the field. Hence, efficiency is a function of time. For purposes of comparison, efficiency was computed over the time necessary to reach saturation. Saturation is defined as the point at which capture events drop to less than one prey item caught per 5-min period *per colony*.

Results

Prey capture around the periphery of a polyp

Figure 1C shows the distribution of particle capture around the polyps on the different tentacles as one moves in the downstream direction; the histograms have been adjusted for the amount of surface area available for prey capture. At low flow speeds ($U_{\text{mean}} = 2.7$ cm/s), prey capture is remarkably asymmetric, with upstream tentacles capturing the most prey [Kolmogorov-Smirnov (K-S) test; $P < 0.001$; $df = 207$]. At intermediate flow speeds ($U_{\text{mean}} = 12.2$ cm/s), the distribution is again asymmetric, but in the opposite direction, with downstream tentacles favored in particle capture (K-S test; $P < 0.001$; $df = 205$). At the highest flow speed tested ($U_{\text{mean}} = 19.8$ cm/s), the distribution is indistinguishable from an even distribution of prey capture around the tentacles (K-S test; $P > 0.5$; $df = 70$). The distribution of capture events is thus markedly affected by flow speed. Only at the highest speeds can capture be modeled by a Poisson process.

Prey capture by tentacles

When prey capture events are examined over the length of individual tentacles, an additional pattern emerges (Fig. 2). At low speeds ($U_{\text{mean}} = 2.7$ cm/s), the distribution is significantly asymmetric, with the outer segments of the tentacles capturing the most prey (K-S test; $P < 0.001$; $df = 207$). The same pattern is found at intermediate flow speeds ($U_{\text{mean}} = 12.2$ cm/s), with the asymmetry shifted even further in the direction away from the pharynx (K-S test; $P < 0.001$; $df = 205$). Finally, at the highest speed used in the flume ($U_{\text{mean}} = 19.8$ cm/s), the distribution is still asymmetric with a bias toward the tentacle tips (K-S test; $P < 0.001$; $df = 70$), but with some differences. Capture in the innermost 20% of the tentacle's length has disappeared, and the outermost 20% experiences much more variable prey capture success.

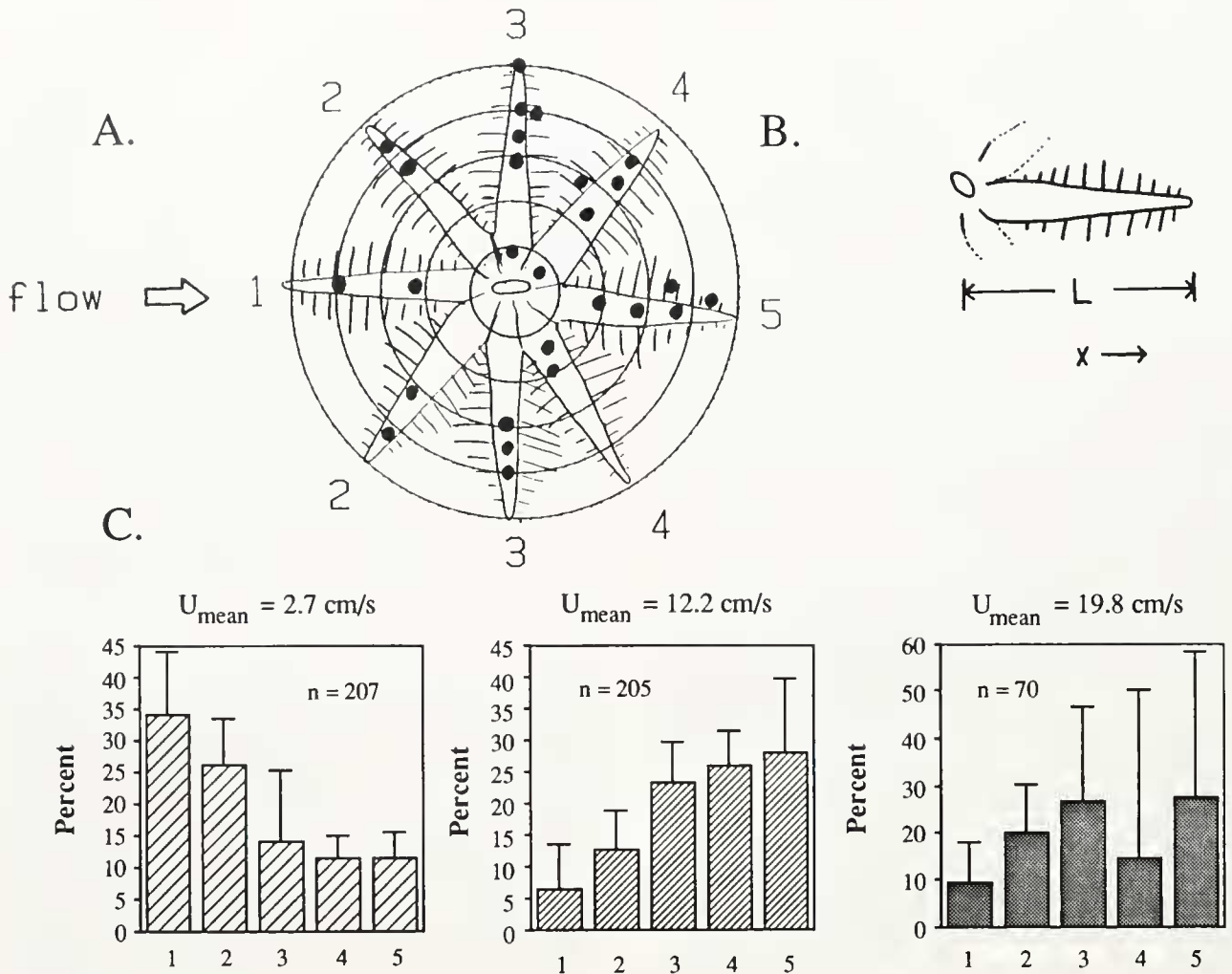
Feeding efficiency

When the efficiency of filtration for individual polyps is examined with respect to Reynolds number (Re) computed for flow around a polyp, a significant inverse relationship is found ($P < 0.05$; $df = 11$), and the efficiency is remarkably low at all speeds tested for feeding in dense concentrations of prey (Fig. 3). $Re = U_{\text{mean}}d/\nu$, where d = polyp oral disk diameter, and ν = kinematic viscosity of seawater. Because polyp size is relatively constant, Re can be viewed as a dimensionless flow speed.

Discussion

Mechanisms of particle impaction

Rubenstein and Koehl (1977) presented dimensionless indices for various mechanisms of particle capture by sus-



Upstream Tentacles ---> Downstream Tentacles

Figure 1. Coordinate system used to quantify prey capture in individual polyps in colonies of *Alcyonium*. (A) Quantification in the circumferential direction around the polyp. Note the pairing of tentacles from the bilaterally symmetric halves of the polyp, *i.e.*, prey caught on tentacles with the same identification number were paired. The five concentric rings delineate the dimensionless length coordinate used for assessing capture by individual tentacles. (B) The distance from the pharynx toward the tentacle tip (X) is divided by the overall length of the tentacle (L) to generate the dimensionless distance (X/L) used as the independent variable (abscissa) in Figure 2. (C) Circumferential position of prey capture events in individual polyps of *Alcyonium* at three different flow speeds. Data from the bilateral halves of the colony are pooled; see Figure 1A for interpretation of abscissa. Capture frequencies are normalized relative to the amount of tentacle area assigned to the numbers one through five. Data were arc-sine transformed and then back-transformed for graphical portrayal. Vertical bars are 95% confidence intervals. For flow speeds of 2.7, 12.2, and 19.8 cm/s, the total numbers of cysts caught were 207, 205, and 70, respectively.

pension feeding organisms. Table I gives these values for polyps of *Alcyonium* feeding on *Artemia* cysts. Note that direct interception or "geometric" interception (Chang, 1973) has the highest value and is thus most likely to be the dominant mechanism of particle capture. For a rigid filter, the efficiency of capture by direct interception should be independent of flow speed (Fuchs, 1964); this

is contrary to the pattern observed. A formulation of the model more appropriate to aqueous suspensions invokes the importance of short-range (London-van der Waals) forces and does not ignore the hydrodynamic resistance that occurs as the particle squeezes fluid from the space between itself and the filter element (Chang, 1973; La-Barbera, 1984). This more refined theory predicts an in-

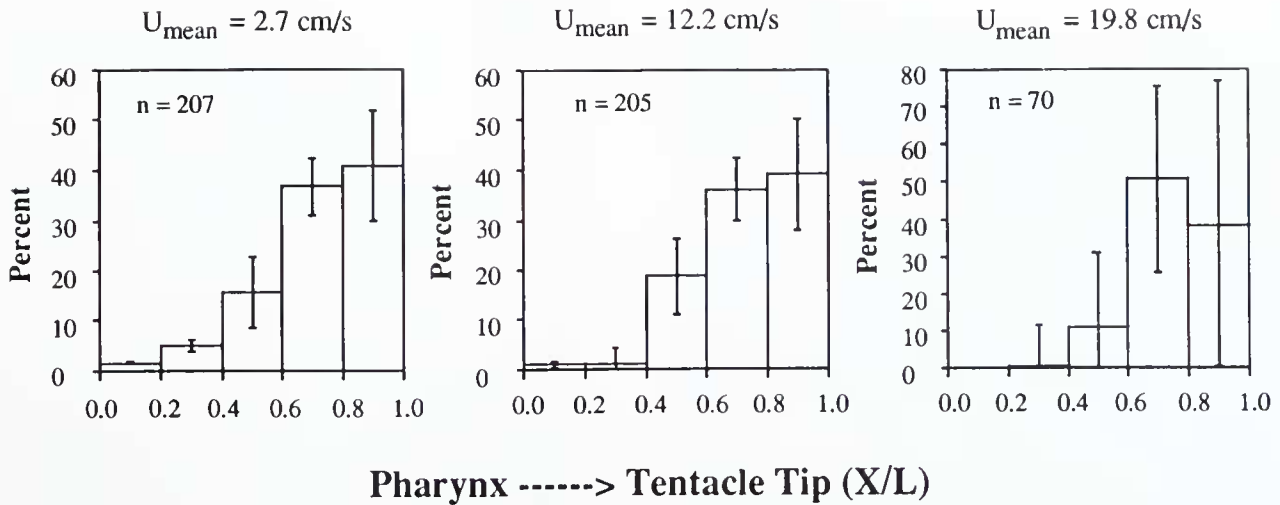


Figure 2. Location of prey capture events along the length of tentacles of polyps in the octocoral *Alcyonium* at three different flow speeds. See Figure 1A for interpretation of abscissa. Capture frequencies are normalized relative to the amount of tentacle area available for prey capture. Data were arc-sine transformed and then back-transformed for graphical portrayal. Vertical bars are 95% confidence intervals. For flow speeds of 2.7, 12.2, and 19.8 cm/s, the total numbers of cysts caught were 207, 205, and 70, respectively.

verse relationship between flow speed at the surface of the filter and efficiency of particle capture and is here observed in *Alcyonium* (Fig. 3). Rubenstein and Koehl (1977) originally predicted that direct interception would be the dominant mode of feeding in aquatic suspension feeders and subsequent work with a diversity of organisms seems to be bearing out their hypothesis (LaBarbera, 1984).

Alcyonium could sieve particles larger than the spacing between pinnules on the tentacles (200–280 μm) as suggested by Sebens and Koehl (1984). However, *Artemia* cysts sieved on the aboral side of a tentacle were almost always dislodged subsequently by the flow and lost to the polyp (pers. obs.). *Artemia* cysts were occasionally sieved by tentacles on the downstream side of the polyp. For larger prey items, sieving may be an important capture mechanism, but probably only for tentacles on the downstream side of a polyp.

The parameter for diffusive deposition assumes the particle has a diffusion coefficient (D) predicted by Brownian motion for a particle of a certain size in a given liquid of a certain temperature and viscosity. If eddy-enhanced diffusion is allowed, the value for D is no longer a constant, but will be a property of the flow speed and eddy size (Richardson, 1926; Okubo, 1971); it can be as much as 10^4 larger than the diffusion coefficient for laminar or "Fickian" diffusion (Okubo, 1980). Turbulent diffusive deposition would increase by a similar factor and would be comparatively more important as the size of the particle of interest decreased, perhaps becoming very important as a mechanism for suspension feeders eating

phyto- and bacterioplankton. Schrijver *et al.* (1981) studied particle collection efficiencies by small glass fibers of about the same diameter as the tentacles in *Alcyonium*. For small particles (*ca.* 5 μm), diffusive deposition was a very significant mechanism. More work is needed in this area, which is technically difficult, because eddy diffusivities near surfaces must be measured (Denny, 1988), and

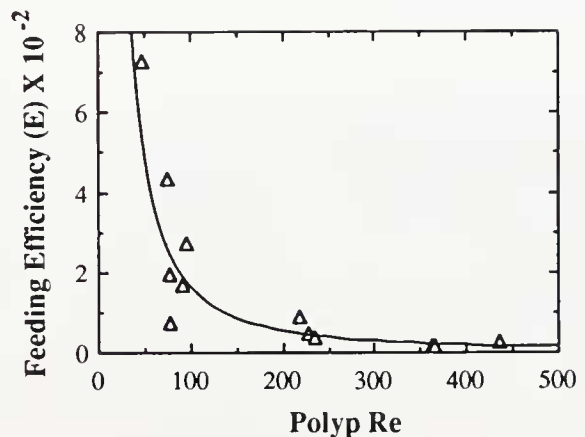


Figure 3. Efficiency (E) of particle capture per polyp in colonies of *Alcyonium* as a function of polyp Reynolds number (Re). Efficiency is defined as the number of particles caught by the polyp in the time interval to saturation of the colony, divided by the number of particles that would have passed through the space occupied by the polyp. Reynolds number was calculated using the oral disk diameter of the polyp and flow speed measured 1.0 cm above the oral disk. Whole colony Re for the specimens used was 10–40 \times greater than polyp Re. The regression is given by the equation: $E = 2066 \text{ Re}^{-1.55}$; $P < 0.05$; $r = 0.92$; $df = 11$.

the convection of unfiltered water to the vicinity of the filter should be considered. Methods of carefully releasing dye and studying its motion near filter feeders using image processing techniques are being developed to allow better investigation of microscale turbulent diffusive deposition (unpub. obs.).

Rates of particle encounter and possible capture by gravitational deposition are independent of flow speed but directly proportional to settling velocity. The settling velocity for *Artemia* cysts is absolutely low, so the total flux of particles to the polyps via this mechanism is much lower than the contribution provided by direct interception. It is unlikely that natural food particles have settling velocities appreciably greater than *Artemia* cysts. The contribution of inertial impaction to the capture of particles at higher Reynolds number could be a potentially important mechanism if particle inertia is appreciable. The upstream side of an individual tentacle will have a stagnation point and the flow will split at this point (Fig. 4) and flow around the tentacle at low flow speeds or up and over the tentacular crown at higher Re (Patterson, 1984). A calculation in the Appendix demonstrates that this mechanism is highly unlikely to be an important mode of particle capture by polyps in this octocoral.

Feeding efficiency of cnidarian filters

The filtration efficiency as calculated *per* Dorman (1966) is very low for individual polyps (Fig. 3); a possible explanation involves partitioning capture efficiency into collection efficiency and adhesion efficiency (Weber *et al.*, 1983). Many particles that appear to strike the surface of

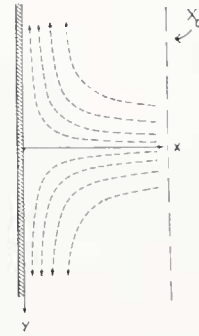


Figure 4. Streamlines of fluid flow near the upstream stagnation point of a filter (Bird *et al.*, 1960), where inertial impaction is most likely to occur. X and Y are directional coordinates. The upstream plane (indicated by X_0) marks where particles carried by the flow have not yet deviated from the streamlines due to their inertia. See the Appendix for a derivation showing how inertial impaction is not likely to be an important capture mechanism for cnidarians that use passive suspension feeding.

Alcyonium tentacles are not trapped; relatively few are lost if they initially adhere, although J. Miles (Northeastern Univ. pers. comm.) found that adhesion and loss was significantly affected by flow speed in the sea anemone, *Metridium senile*, and Leonard *et al.* (1988) found that flow speed affected capture probabilities in a crinoid. My study of capture at the level of the polyp addresses successful prey capture events only.

Future work on the mechanisms of particle capture by cnidarians should investigate the role of unsuccessful adhesions. In particular, the importance of London-van der Waals forces *versus* nematocyst firing should be ex-

Table 1

Values of dimensionless parameters for four potential modes of particle capture (*cf.* Rubenstein and Koehl, 1977) in the octocoral *Alcyonium siderium* feeding on *Artemia* cysts at two different flow speeds commonly encountered in nature

| | Gravitational deposition | Direct interception | Inertial impaction | Diffusive deposition |
|-------------------|----------------------------|----------------------------|--|------------------------------|
| | $N_{gd} = \frac{U_g}{U_0}$ | $N_{di} = \frac{d_p}{d_r}$ | $N_i = \frac{(\rho_p - \rho_m) d_p^2}{18 \mu d_r}$ | $N_{dd} = \frac{D}{d_r U_0}$ |
| $U_0 = 3.0$ cm/s | 0.027 | 0.67 | 4.0×10^{-6} | 8.2×10^{-11} |
| $U_0 = 30.0$ cm/s | 0.003 | 0.67 | 4.0×10^{-5} | 8.2×10^{-12} |

d_p = particle diameter = 0.02 cm (Patterson, 1984).

d_r = filter element diameter = 0.03 cm (Sebens and Koehl, 1984).

U_g = Stokes' settling velocity = 0.08 cm/s (Gibbs, 1985).

ρ_p = density of particle = 1.05 g/ml (Gibbs, 1985).

ρ_m = density of seawater = 1.02 g/ml at 10°C (Zerbe and Taylor, 1953).

μ = dynamic viscosity of seawater = 1.4×10^{-2} g/(cm·s) at 10°C (Sverdrup *et al.*, 1942).

U_0 = flow near the tentacle (two values used in table above; *cf.* Patterson, 1984; Patterson and Sebens, 1989).

D = diffusion coefficient of an *Artemia* cyst = $\frac{KT}{6\pi\mu d_p} = 7.4 \times 10^{-12}$ cm²/s.

KT = energy of thermal fluctuation = 3.9×10^{-14} (g·cm²)/s².

plored, as current data are insufficient to address this issue. The subject bears further attention because Best (1988) also found that feeding efficiency was an inverse function of flow speed (read Reynolds number) in the sea pen, *Ptilosarcus gurneyi*. She attributed this decline to the predicted behavior of particles that are caught by direct interception (Spielman, 1977), perhaps aided by a deformation of the filter elements as the hydrodynamic drag increased. *Alcyonium* polyps on the upstream side of colonies deform in strong flows while polyps in the wake undergo little deformation (Patterson, 1984). The octocorals she studied are more efficient than *Alcyonium* by a factor of five at a similar flow speed. This study used only polyps located near the top of the colony. Increasing mechanical deformation of this subpopulation of polyps occurred at higher flows, resulting in less surface area available for prey capture, but the reduction was detected in the measurements of projected colony surface area. The reasons for this interspecific difference in feeding effectiveness are presently unknown.

Particle capture locations

The patterns of prey capture seen (Figs. 1C, 2) are in agreement with a direct interception model of prey capture. Polyps resemble inverted umbrellas (see photograph in Sebens and Koehl, 1984); they do not hold their tentacles in a flat canopy as the top view in Figure 1A might imply. At low speeds, the first tentacles to encounter particles are the upstream ones, and here capture is more likely. As the flow speed increases, the polyps are bent by the flow (*cf.* Patterson, 1984), and the aboral side of the upstream polyps is presented to the flow. For prey particles the size of *Artemia* cysts (*ca.* 200 μm ; close in value to the mean size of natural zooplankton prey, Sebens and Koehl, 1984), few particles are caught on these upstream tentacles because particles do not adhere to the aboral side. The downstream tentacles then begin feeding. In strong flows, the polyp is severely bent downstream, and a small eddy forms over the tentacular disk (*pers. obs.*); the distribution becomes roughly symmetric again. The relative roles that attached eddy formulation and turbulent diffusion play in this smoothing out of the particle capture distribution are unknown.

These experiments were conducted under turbulent but steady flow conditions. *Alcyonium* occurs over a range of depths and habitats in the shallow subtidal; it is exposed to both oscillatory flow from wind-driven waves and to steady tidal flows (Patterson, 1984, 1985). The particle capture behavior of individual polyps and tentacles might be quite different in an oscillating flow. Hunter (1989) found that the feeding effectiveness of the hydroid *Obelia longissima* was much greater in an oscillating flow relative to a steady current. *Alcyonium* colonies are inherently

more rigid than those of *Obelia*, and hence it is not clear without further experimentation whether oscillatory flow would result in enhanced feeding in *Alcyonium*. Thus these results should be applied only to feeding in the field under steady flow conditions when wind-driven oscillations have a small contribution to the flow field.

The distribution of particle capture over the length of an individual tentacle is also in agreement with a geometric (direct) interception model. Parts of the tentacle furthest out of the boundary layer of the polyp intercept the most prey. Patterns of prey capture discerned through flume experiments using non-motile particles such as *Artemia* cysts may be different from those measured using live prey, but only if the loss rate of captured particles differs between the two types of food or the motility of live prey causes the diffusive deposition mechanism to increase capture preferentially at a location different from direct interception. Loss of captured particles is most likely caused by hydrodynamic drag forces exceeding the breaking strength of the attachment between particle and tentacle. Live zooplankton prey and *Artemia* cysts will experience very similar amounts of drag because size and shape are similar. The motility of live zooplankton should result in an increase in the diffusive particle flux relative to *Artemia* cysts, but it should not affect the geometric location of capture on tentacles if movement is random in all directions.

This study has shown how flow regime can dramatically affect patterns of particle capture at the level of the filtering elements in an octocoral. Variation in feeding ability at the level of the polyp caused by hydrodynamics may help explain the variation Lasker (1981) observed in prey capture between polyps and branches in colonies of tropical gorgonians. Capture events in the three species Lasker studied did not fit a Poisson distribution, and he invoked differential feeding ability of the polyps as the cause of the variation. He offered no explanation for the differential feeding ability other than to note that other authors had also seen asymmetric patterns in prey capture by cnidarians (*e.g.*, Laversee, 1976). I have demonstrated that momentum transport (fluid flow) directly affects mass transport (particle capture) at the level of the individual feeding elements, polyps. Upon closer inspection, other passive suspension feeding cnidarians may exhibit similar patterns.

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Appendix

The following derivation, developed from the work of Glauert (1940) on raindrop capture by airfoils and from Taylor (1940) on aircraft icing, shows how unlikely it is that inertial impaction will be an important mechanism for passive suspension feeding cnidarians for the range of velocities normally encountered in the field.

Consider the motion of a solid particle (*e.g.*, a plankter), moving with a velocity relative to the seawater, as it approaches the upstream end of a filtering organism (Fig. 4). In other words, the particle does not follow the streamlines perfectly. If the Reynolds number (*Re*) of the particle is on the order of one or less, as it would be for plankton-size particles (Koehl and Strickler, 1981), the forces acting on the particle are due solely to the Stokes' drag (Berg, 1983). The equation governing the motion of the particle in the *x*-direction is:

$$\frac{4}{3} \pi r^3 \rho_s \frac{dU_p}{dt} = 6 \pi r \mu (U - U_p) \quad (\text{Eq. 1})$$

where *r* = particle radius, ρ_s = particle density, μ = dynamic viscosity, U_p = velocity component of the particle in the *x*-direction, and *U* = velocity component of the seawater in the *x*-direction.

The velocity components in the *y*- and *z*-directions are *V* and *W*, respectively, and the equations of motion are similar. If I define:

$$k_0 = \frac{2\rho_s r^3}{9\mu} \quad (\text{Eq. 2})$$

then (Eq. 1) becomes:

$$k_0 \frac{dU_p}{dt} = U - U_p \quad (\text{Eq. 3})$$

and other directions can be transformed similarly.

The equations of motion must be solved subject to the initial conditions. Let me introduce a scaled time variable,

$$T = \frac{t}{k_0} \quad (\text{Eq. 4})$$

and the differential operator,

$$\frac{d}{dT} = k_0 \frac{d}{dt} \quad (\text{Eq. 5})$$

Now (Eq. 3) becomes

$$\frac{dU_p}{dT} = U - U_p \quad (\text{Eq. 6})$$

and similarly for the other directions.

Flow near the upstream stagnation point of the filter will look like Figure 4 (Bird *et al.*, 1960). The velocity field near the stagnation point is given by:

$$U = -cx \quad (\text{Eq. 7})$$

and

$$V = cy \quad (\text{Eq. 8})$$

Substituting into (Eq. 6), I obtain:

$$\frac{d^2x}{dT^2} + \frac{dx}{dT} + ck_0x = 0 \quad (\text{Eq. 9})$$

It is reasonable to assume that upstream of the tentacle a certain distance, X_0 , the flow field is not distorted by the presence of the tentacle and the particle is following the streamlines of the moving seawater (see Fig. 4). If the time at which the particle starts to deviate from the streamlines of flow is called $T = 0$, I obtain:

$$x(0) = -X_0 \quad (\text{Eq. 10})$$

$$\frac{dx}{dT} = ck_0X_0 \quad (\text{Eq. 11})$$

A reasonable guess to the solution of (Eq. 11) is one of the form $x(t) = Ae^{pt}$, where *A* = constant. The characteristic equation is thus,

$$p^2 + p + ck_0 = 0 \quad (\text{Eq. 12})$$

The roots of the equation are:

$$p_{1,2} = \frac{-1 \pm \sqrt{1 - 4ck_0}}{2} \quad (\text{Eq. 13})$$

When one of the roots is imaginary, the solution to the equation of motion of the passing particle will be oscillatory, *i.e.*, the particle position and the filter position will eventually coincide ($x = 0$). This condition will occur when:

$$4ck_0 > 1 \quad (\text{Eq. 14})$$

Glauert (1940) showed for a cylindrical geometry that a negligible number of particles will impact if $k_0c \leq 0.125$, where $c = 2$ and the definition of k_0 is as follows:

$$k_0 = \frac{2\rho_s r^2 R U}{9\rho R^2 \nu} \quad (\text{Eq. 15})$$

where R = radius of the filter, and $\nu = \mu/\rho$, the kinematic viscosity of the seawater.

Using reasonable values for flow around an *Alcyonium* colony, I obtain $k_0c = 0.003$, for $\rho = 1.024 \text{ g/cm}^3$, (Zerbe and Taylor, 1953), $\rho_s = 1.049 \text{ g/cm}^3$, (Gibbs, 1985), $r = 100 \times 10^{-4} \text{ cm}$, $R = 5 \text{ cm}$, $U = 5 \text{ cm/s}$, $\nu = 1.36 \times 10^{-2} \text{ cm}^2/\text{s}$ for seawater at 10°C (calculated from Sverdrup *et al.*, 1942). If the flow speed increases by an order of magnitude to $U = 50 \text{ cm/s}$, then $k_0c = 0.034$. Appreciable impaction will not occur until $U = 185 \text{ cm/s}$, far above the range of speeds normally encountered near this species (Patterson and Sebens, 1989). Such a flow would only be found under stormy conditions in the subtidal or in tidal currents in fjords. *Alcyonium* contracts its prey-capturing surfaces long before this flow speed is obtained (Patterson, 1980).